MICROHABITAT USE AND PREDATOR RECOGNITION BY THE HISPID POCKET MOUSE, *CHAETODIPUS HISPIDUS*

By

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PREFACE

The two chapters composing this thesis have been formatted for independent publication. The first chapter, "Seasonal microhabitat use by the hispid pocket mouse, *Chaetodipus hispidus*", will be submitted to *The Southwestern Naturalist*. The second chapter, "Use of chemosensory cues by the hispid pocket mouse, *Chaetodipus hispidus*", to recognize snake predators, will be submitted to *Animal Behaviour*.

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CHAPTER I

SEASONAL MICROHABITAT USE BY THE HISPID POCKET MOUSE, *CHAETODIPUS HISPIDUS*

ABSTRACT- A variety of factors influence microhabitat selection by animals. Types of microhabitats used are determined by the natural history traits of an animal and can be influenced by predators. I used the powder tracking method to follow movements of hispid pocket mice, *Chaetodipus hispidus*, during the warm season when snakes were active and the cold season when they were dormant. I used compositional analysis to compare microhabitat use to that available. During the warm season, pocket mice used bare ground and short grass significantly more than tall grass or shrub. During the cold season, pocket mice were not as selective and only used bare ground significantly more than tall grass. Areas with little to no vegetation may be preferred when snakes are active so that mice can detect and avoid encountering them in dense vegetation. During the cold season, other factors such as food abundance and avian predators may influence pocket mice to use tall grass and shrub habitats where risk of predation should be lower.

INTRODUCTION-A variety of factors influence microhabitat selection by animals. Types of microhabitats used are determined by the natural history of an animal and can be influenced by predators (e.g., Rosenzweig, 1973; Kotler, 1984; Brown et al., 1988).

Rodents are a primary prey item for many species, including birds of prey, mesocarnivores, and snakes. Microhabitat selection by rodents may depend on the predator to be avoided. For example, field voles (*Microtus agrestis*) prefer areas of cover when avian predators are detected (Korpimäki et al., 1996), and kangaroo rats (*Dipodomys deserti*) avoid bush habitat more than open or grass habitat when the scent of a snake is present (Bouskila, 1995).

Snakes can affect foraging behavior of rodents by reducing time spent at a foraging location when cues for snakes are present and by shifting microhabitat preference by rodents (Bouskila, 1995). Snakes also may be responsible for a seasonal shift in microhabitat use that corresponds with their hibernation period; desert rodents prefer open habitat in the summer and shift to bush or smaller open spaces in the winter (Brown, 1989; Price, 1978).

The hispid pocket mouse is a heteromyid rodent whose range extends from North Dakota, through the plains states, and into central Mexico. The species is found in grassland and shrubland habitats with sandy soils (Paulson, 1988). Predators of hispid pocket mice include barn owls (*Tyto alba*), great horned owls (*Bubo virginianus*), coyotes (*Canis*

latrans), raccoons (*Procyon lotor*), and various snake species including bullsnakes (*Pituophis*), ratsnakes (*Elaphe*), kingsnakes (*Lampropeltis*), and rattlesnakes (*Crotalus*--Brown and Harney, 1993). Hispid pocket mice are nocturnal, quadrupedal locomotors, and granivorous foragers that live in burrows during the day. Studies demonstrating microhabitat association of some *Chaetodipus* species have been conducted. For example, Price (1978) showed that *C. baileyi* and *C. penicillatus* were trapped more frequently under large bushes and trees than in open habitat. M'Closkey (1978) found that *C. baileyi* used more open habitat than *C. penicillatus*, and Rosenzweig and Winakur (1969) suggested that *C. hispidus* required dense, high grass, *C. penicillatus* depended on bush or shrub habitat, and *C. baileyi* required shrubs and trees. Additional studies also have reported that quadrupedal heteromyids preferred areas with cover (e.g., Rosenzweig, 1973; Reichman and Price, 1993). However, little is known about the natural history of hispid pocket mice. Despite this species' abundance and extensive distribution which encompasses several microhabitat types, information regarding what microhabitats this species prefers is lacking.

The purpose of this study was to investigate what microhabitats hispid pocket mice prefer and to determine if they display a shift in microhabitat use that corresponds with season.

METHODS-*Study site*-The study site was located ca. 56 km N of Woodward, Oklahoma, on private land and at the adjacent Selman Wildlife Management Area (SWMA) in Woodward Co. Much of the land was composed of sandy soils, and dominant plant species included little blue stem (*Schizachyrium scoparium*), buffalo grass (*Buchloe dactyloides*), sand sage (*Artemisia filifolia*), sand plum (*Prunus angustifolia*), and shin oak (*Quercus havardii*). Small mammals documented on the management area included the hispid pocket mouse, silky pocket mouse (*Perognathus flavus*), fulvous harvest mouse (*Reithrodontomys fulvescens*), white-footed mouse (*Peromyscus leucopus*), deer mouse (*P. maniculatus*), hispid cotton rat (*Sigmodon hispidus*), and several bat species including a large colony of Mexican free-tailed bats (*Tadarida brasiliensis*) that resided on the area in the summer (Caire et al., 1989). Snake species that occurred in this area included the diamondback rattlesnake (*Crotalus atrox*), prairie rattlesnake (*Crotalus viridus*), speckled kingsnake (*Lampropeltis getulus*), bullsnake (*Pituophis melanoleucus*),

ringneck snake (*Diadophis punctatus*), and western coachwhip (*Masticophis flagellum*--Conant and Collins, 1998).

Microhabitat availability and use-To assess available microhabitat types used by pocket mice, I set 200-300 Sherman live traps during summer and fall of 2002 and 2003 (3,600 total trap nights) solely during the new moon. Moonlight has been shown to affect habitat selection and activity in several species of rodents (Lockard and Owings, 1974*a*, 1974*b*; Kaufman and Kaufman, 1982; Kotler, 1984; Price et al., 1984; Bowers, 1986; Mandelik et al., 2003), and I wanted to avoid confounding results due to differing light intensities. I set traps for 16 trapping periods, for 1, 2, or 3 consecutive nights in duration depending on trap success the previous night. I set 4-6 trap lines that consisted of 50 traps each and placed them in grassland/shrub habitat in five sections of the study area (Fig. 1). I placed trap lines ≥ 10 m apart with traps 5 m apart within a trap line and baited them with rolled oats.

To determine microhabitat availability, I used a modification of the line-intercept technique (Canfield, 1941) to sample microhabitat type at every tenth trap station starting with the first trap and ending with the last for each line. I held two 2-m poles placed perpendicular to each other at their mid-points and placed

them directly over each station to form a transect. I determined the direction in which the poles were placed, either North/South-East/West or Northeast/Southwest-Northwest/Southeast, by the flip of a coin. I then recorded microhabitat types along the pole transects. Microhabitat types I quantified were bare ground, short grass, tall grass, shrubs, and trees. Bare ground included areas of dirt or sand, short grass included grasses ≤ 0.3 m tall and areas containing sparse clumps of grassy vegetation or litter, tall grass included grasses > 0.3 m tall, shrubs included woody vegetation ≤ 1.5 m tall, and trees included woody vegetation > 1.5 m tall. I recorded mice as using the taller microhabitats (tall grass, shrub, and tree) if they traveled under or through them.

I assessed microhabitat use by means of the powder tracking method (Lemen and Freeman, 1985). I powder tracked 13 (4 female, 5 male, 4 unknown) pocket mice for 510.31 m during the warm season (when snakes were active) and 8 (5 female, 3 male) mice for 201.78 m during the cold season (when snakes were inactive). I determined warm and cold seasons by comparing temperatures at which rattlesnakes were active with low temperatures during the trapping session. The optimum temperature range for normal rattlesnake activity is between 26.5°C and 32°C (Klauber,

1997). The maximum temperature that a rattlesnake can withstand is 43.3°C, and the minimum temperature at which a rattlesnake will voluntarily move is 16.1°C (Klauber, 1997). I therefore considered trapping sessions during June through October to be warm season (lowest temperature 14.4°C) and sessions in November to be cold season (highest low temperature 8.8°C). I confirmed high and low temperatures by measuring air temperature at the end of each powder tracking session (ca. 2300 hours) using a thermometer.

I set Sherman traps at dusk, checked them the next morning, marked pocket mice with numbered monel ear tags and held them in individual Sherman traps until dusk. At dusk, I dusted mice with fluorescent, non-toxic powder and released mice at the site of capture (Menzel, et al., 2000). The next night I used a hand-held ultraviolet light to follow the powder trail. Each time the trail changed direction I marked it with a flag so that in daylight I could measure the trail. The next morning I followed the flag trail and recorded distances in each microhabitat type. To account for escape behavior and microhabitats used in response to the release of the mouse, I deducted 2 m from the beginning of each trail. I generated proportions of microhabitats used and available, during

both warm and cold seasons, and compared them using compositional analysis (Aebischer et al., 1993). This analysis transforms use and availability data to log ratios and uses a multivariate analysis of variance procedure to determine if differences in use and availability are different than zero ($P < 0.05$). Because log ratios are used, I replaced zero values in my data set with 0.0001 to avoid null proportions. I chose this replacement value because it is less than the smallest nonzero value in my data set (Aebischer et al., 1993). Compositional analysis then ranks habitats in order of relative preference, zero indicating the least preferred habitat type. Significant differences in habitat use are determined by calculating a t-value from the ratio mean and standard error (Aebischer et al., 1993).

RESULTS– At SWMA, I caught the hispid pocket mouse, deer mouse, white-footed mouse, hispid cotton rat, fulvous harvest mouse, silky pocket mouse, eastern mole, woodrat, prairie vole (*Microtus ochrogaster*), and northern grasshopper mouse (*Onychomys leucogaster*). I recaptured 3 hispid pocket mice. On SWMA, I encountered five diamondback rattlesnakes, 1 speckled kingsnake, and 1 western coachwhip.

Warm season-Tree microhabitat was least available of habitats measured, ranging from 0% to 3.6%. Of the 13 pocket mice tracked, 1 used tree microhabitat for 24.5% of its total microhabitat use. Rankings for microhabitat selection during the warm season show tree is ranked 1 and is used significantly more than shrub (Table 1A). These results are likely due to the fact that compositional analysis has been shown to inflate the Type I error rate when available habitat is not used by animals (Bingham and Brennan 2004). Additionally, Bingham and Brennan (2004) found that the degree of Type I error rate inflation is a function of the substitution value and that the smaller the substitution value, the higher the Type I error rate. I used 0.0001 to substitute for 0 values, probably causing the Type I error rate to be high. Because tree was least available and seldom used, it was dropped from the data set and proportions were reanalyzed.

When tree was removed from the dataset, microhabitat use by hispid pocket mice was nonrandom (Lambda = 0.36, X^2 = 13.26, $P < 0.05$; Table 1B). Nonrandom use is evident when comparing ranking of habitats to proportions of available habitat and their averages (Table 2A). For example, bare ground was most preferred even though it was least abundant

and short grass was ranked second in preference despite it being most abundant.

Overall, bare ground was most preferred and was used significantly more than tall grass and shrub. Short grass was ranked second and was used significantly more than tall grass and shrub. Tall grass was ranked third and shrub fourth although not significantly different from each other.

Cold season-Tree microhabitat was the least available habitat measured, ranging from 0% to 0.58%. Of the 8 pocket mice tracked, 1 used tree microhabitat for 0.4% of its total microhabitat use. Table 3A shows the matrix of rankings for microhabitat selection during the cold season. Tree is ranked 3 (preferred second). Again, these results are likely due to compositional analysis and the low substitution value I used (0.0001), which has been shown to inflate the Type I error rate (Bingham and Brennan 2004). Because tree was least available and seldom used, it was dropped from the data set and proportions were reanalyzed.

When tree was removed from the dataset, microhabitat use by hispid pocket mice in the cold season was nonrandom (Lambda = 0.24, $X^2 = 11.35$, $P < 0.05$). The matrix of rankings for microhabitat selection is reported in Table 3B. Nonrandom use was evident when comparing the ranking

of habitats to proportions of available habitat and their averages (Table 2B). For example, bare ground was most preferred even though it was only second most abundant and short grass was least preferred despite that it was most abundant.

Overall, bare ground was most preferred and was used significantly more than tall grass. Shrub was ranked second, tall grass third, and short grass fourth, although they did not differ significantly from each other.

DISCUSSION—Rodents are primary prey for many species, making it likely that threat of predation greatly influences habitat selection by rodents. Hispid pocket mice displayed different habitat preferences during seasons in which snakes were active and inactive. During the warm season, areas consisting of tall grass and shrub were avoided while areas with short grass or no vegetation were preferred. During the cold season, bare ground was preferred more than tall grass but no other significant differences in habitat use were detected.

Pocket mice were more selective about microhabitat use during the warm season when snakes were a threat. Many snake species employ a sit-and-wait tactic that involves hiding under vegetation and striking at prey that pass by (Reinert et al., 1984; Werler and Dixon, 2000). Pocket

mice may use bare ground more so they can detect and avoid encountering snakes that may be present under shrubs. They also may be able to use safer microhabitats such as bare ground because food is abundant and the benefit of foraging in dense vegetation does not out-weigh the risk of predation.

Pocket mice were not as selective during the cold season. They may be exploiting other habitats in search of food because this resource is scarce. Threat of snakes is decreased so they can use different microhabitats without risk. Additionally, vegetated habitat has been shown to be preferred under threat of avian predators (Abramsky et al., 1996; Korpimaki, 1996). Owls may be greatly influencing microhabitat selection, especially because other prey items (i.e., Mexican free-tailed bats; personal observation) are absent at the site during the cold season.

During warm and cold seasons, bare ground was most preferred, which also may be in response to owl predation. Owls use hearing to locate prey, especially under low-light conditions that are present during the new moon (Knudsen, 1980; Konishi, 1983). Pocket mice may choose to travel on bare ground so that noise produced by rustling vegetation is limited thereby making detection by owls more difficult, although no studies to my knowledge have directly addressed

this issue and capture success is lower in vegetated habitat (Longland and Price, 1991). Additionally bare ground may be safer to use during the new moon because visibility by owls is reduced, making prey capture more difficult (Longland and Price, 1991).

Bouskila (1995) found that when sidewinder (*Crotalus cerastes*) scent was present, *Dipodomys deserti* avoided bush habitat more than open or grass habitat, indicating that the mice associated bush habitat with a higher risk from snakes. Brown (1989) and Price (1978) demonstrated that *D. merriami* preferred open habitat in summer but shifted toward bush in winter, corresponding with changes in levels of activity by snakes.

Heteromyids using quadrupedal locomotion may restrict their activities to areas with vegetation cover where predation risk is lower because they lack the ability to maneuver and avoid predation quickly like bipedal heteromyids (Bartholomew and Caswell, 1951; Rosenzweig, 1973; Kotler, 1984). This has been demonstrated in the desert, where open areas are more abundant than vegetated areas. In grassland areas, however, vegetation is quite abundant, and quadrupedal rodents may be able to exploit open areas because the protection that vegetation offers is nearby.

The results of this study demonstrate that hispid pocket mice do select among available microhabitat types. Avian predators and food availability likely influence seasonal changes in habitat preference. However, the absence of snakes, primary predators, during part of the year may allow pocket mice to exploit different habitats that would otherwise be associated with high risk. Differences in microhabitat use between warm and cold seasons coincide with changes in snake activity, suggesting that avoidance of snakes plays a role in microhabitat selection by these mice. Further research addressing if pocket mice can detect the presence of predatory snakes may help determine if they rely on microhabitat selection to avoid predation.

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TABLE 1. Matrix of microhabitat rankings for summer with and without tree included in analysis. Positive values indicate the habitat of the row was used relatively more than the habitat of the column; negative values indicate the row was used less. A 3 signifies a significant difference in use between habitats whereas a 1 denotes no significance.

Microhabitat	Rank	Bare	Short grass	Tall grass	Shrub	Tree
Bare	4		1	3	1	3
Short grass	0	-1		-1	-1	-1
Tall grass	1	-3	1		-1	-1
Shrub	2	-1	1	1		-1
Tree	3	-3	1	1	1	
Bare	3		1	3	3	
Short grass	2	-1		3	3	
Tall grass	1	-3	-3		1	
Shrub	0	-3	-3	-1		

TABLE 2. Ranges and means of available habitat across sampling times during summer (A) and winter (B).

	Bare	Short grass	Tall grass	Shrub
A.				
Range	8.34% - 17.36%	33.07% - 50.99%	21.25% - 30.71%	17.31% - 27.61%
Mean	12.63%	43.08%	22.79%	21.49%
B.				
Range	5.23% - 25.10%	36.79% - 51.14%	16.25% - 18.39%	19.72% - 27.39%
Mean	22.62%	38.58%	18.12%	20.67%

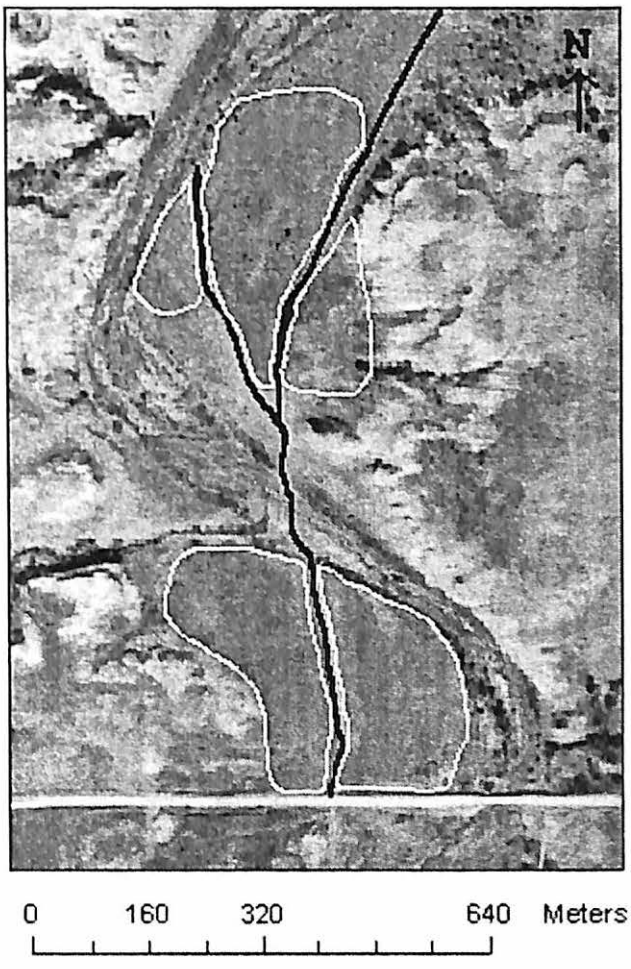
TABLE 3. Matrix of microhabitat rankings for winter with and without tree included in analysis. Positive values indicate the habitat of the row was used relatively more than the habitat of the column; negative values indicate the row was used less. A 3 signifies a significant difference in use between habitats whereas a 1 denotes no significance.

Microhabitat	Rank	Bare	Short grass	Tall grass	Shrub	Tree
Bare	4		1	3	1	3
Short grass	0	-1		-1	-1	-1
Tall grass	1	-3	1		-1	-1
Shrub	2	-1	1	1		-1
Tree	3	-3	1	1	1	
Bare	3		1	3	1	
Short grass	0	-1		-1	-1	
Tall grass	1	-3	1		-1	
Shrub	2	-1	1	1		

Figure legend

Fig. 1. Aerial photograph of Selman Wildlife Management Area and surrounding private land. Trapping areas are outlined in white.

Figure 1



CHAPTER II

USE OF CHEMOSENSORY CUES BY THE HISPID POCKET MOUSE, *CHAETODIPUS HISPIDUS*, TO RECOGNIZE SNAKE PREDATORS

ABSTRACT-Animals use auditory, visual, tactile, and olfactory signals to detect and avoid predators. Several mammalian species have been shown to recognize scents of mammalian and reptilian predators. I examined how hispid pocket mice respond to the scent of a sympatric snake predator, allopatric snake predator, non-predatory snake, and non-predatory mammal. I exposed mice to each scent over a four-day period (one scent per day) in a laboratory apparatus containing two chambers: with a test scent and with a control. I recorded number of times mice went into the scent or control chamber and the proportion of time spent in either chamber. Repeated measures ANOVA showed no differences in number of times mice entered chambers in any test. There also were no significant differences in time spent in chambers with sympatric predator scent, non-predatory mammalian scent, non-predatory mammalian scent, and their corresponding controls. Pocket mice did, however, spend significantly more time in the chamber with allopatric predator scent than in the control chamber. They may have spent more time with this scent for investigation because it was unfamiliar. Response to sympatric predator scent indicates that chemosensory cues alone may not be threatening enough to elicit avoidance or inspection of the scent. Pocket mice likely use other

means to avoid snake predation such as selective microhabitat use.

Predator recognition and avoidance are crucial for survival. Animals may use visual, auditory, tactile, and olfactory cues to identify predators and minimize risk by making appropriate behavioural decisions to avoid predation. Several studies have demonstrated that mammals can detect mammalian predators using chemosensory cues (e.g. Dickman 1992; Ward et al. 1997; Wolff & Davis-Born 1997; Borowski 2000; Herman & Valone 2000; Jones & Dayan 2000; Pusenius & Ostfeld 2002). Because rodents are primary prey for several snake species, they likely have evolved ways of detecting and avoiding snakes. Chemosensory cues may be particularly important for nocturnal rodents because auditory and visual information may be difficult to detect. Most snakes excrete pheromones that aid in locating potential mates (Mason 1992). Some species also use chemical cues for interspecific recognition (Halpern 1992). These pheromones, along with other odours, may be detected by prey.

The hispid pocket mouse is a North American heteromyid rodent whose range extends from North Dakota, through the plains states of the central U.S., and into central Mexico.

This species is found in grassland and shrubland habitats with sandy soils and may be quite abundant in areas with suitable habitat (Paulson 1988). These mice are nocturnal, quadrupedal locomotors and granivorous foragers that live in burrows during the day. Predators of hispid pocket mice include barn owls (*Tyto alba)*, great horned owls (*Bubo virginianus*), coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and various snake species including bullsnakes (*Pituophis*), ratsnakes (*Elaphe*), kingsnakes (*Lampropeltis*), and rattlesnakes (*Crotalus*--Brown & Harney 1993). Studies comparing desert-dwelling bipedal and quadrupedal heteromyids suggest that quadrupedal species such as *Chaetodipus* spend more time under cover of vegetation and less time in the open because they lack the speed and agility to avoid avian predators (Bartholomew & Caswell 1951; Thompson 1982; Kotler 1984; Longland & Price 1991). Concentrating foraging efforts in dense vegetation, however, leaves them susceptible to predators such as snakes that also may be under vegetation. Snake species such as rattlesnakes employ a sit-and-wait foraging strategy to capture their prey (Werler & Dixon 2000). They wait under bushes and trees or in grass where their cryptic color pattern allows them to escape detection by potential prey (Reinert et al. 1984; Werler & Dixon 2000).

Rattlesnakes have a diverse diet, typically selecting their food items based on size and not necessarily preying upon the most abundant species in the area (Werler & Dixon 2000). They frequently prey on small mammals, including pocket mice (Klauber 1997). Cottam (1959) reported that hispid pocket mice were the primary food of the diamondback rattlesnake (*C. atrox)* in south Texas.

Studies have been conducted on some bipedal heteromyid species regarding snake detection and avoidance. Bouskila (1995) found that *Dipodomys deserti* reacted to sidewinder scent (*Crotalus cerastes*) by collecting fewer seeds where scent was present and avoiding bush habitat more than open or grass habitat when scent was detected. Randall et al. (1995) showed that *D. merriami* and *D. spectabilis* react differently to presence of a snake predator. *Dipodomys. merriami* avoided a gopher snake, but *D. spectabilis* approached the snake, jumped back to avoid a strike, and then footdrummed. Ackland (2004; Chapter 1) demonstrated that hispid pocket mice were less selective in type of microhabitat used during the cold season when rattlesnakes were inactive compared with the warm season when they were active. No studies have considered a quadrupedal heteromyid such as the hispid pocket mouse and its reaction to the scent of a predator. Because rattlesnakes are a

primary predator of pocket mice, use a sit-and-wait foraging strategy, and excrete various chemical cues, it is plausible that pocket mice have evolved to use olfaction to detect rattlesnakes. The purpose of this study was to determine if 1) pocket mice distinguish between snake odour and a control, 2) pocket mice respond differently to the scents of a predator snake and a non-predator snake, and 3) pocket mice respond differently to the scent of a snake predator that is sympatric as opposed to a snake predator that is not sympatric.

METHODS

Study Areas

I collected mice and snakes from three study sites. The Selman Wildlife Management Area and adjacent private land (SWMA), in Woodward Co., was located ca. 56 km N of Woodward, Oklahoma in the south-central U.S. The Selman Living Laboratory (SLL), part of the University of Central Oklahoma, was ca. 3.22 km S and 3.22 km W of the SWMA, also in Woodward Co. The third site, STILL, was on private land ca. 3 km NE of Stillwater in Payne Co., Oklahoma.

Small mammals present on SWMA and SLL included the hispid pocket mouse, silky pocket mouse (*Perognathus flavus*), fulvous harvest mouse (*Reithrodontomys fulvescens*), white-footed mouse (*Peromyscus leucopus*), deer

mouse (*P. maniculatus*), hispid cotton rat (*Sigmodon hispidus*), eastern mole (*Scalopus aquaticus*), and woodrat (*Neotoma albigula*--Caire et al. 1989). Snake species that occurred in this area included the diamondback rattlesnake, prairie rattlesnake (*Crotalus viridus*), eastern hognose snake (*Heterodon platyhinos*), speckled kingsnake (*Lampropeltis getulus*), bullsnake (*Pituophis melanoleucus*), western coachwhip (*Masticophis flagellum*), western ribbon snake (*Thamnophis proximus*), and ringneck snake (*Diadophis punctatus*--Conant & Collins 1998).

Small mammals present at STILL were the hispid pocket mouse, fulvous harvest mouse, white-footed mouse, deer mouse, and hispid cotton rat (Caire et al. 1989). Snake species in this area included the timber rattlesnake (*Crotalus horridus*), copperhead (*Agkistrodon contortrix*), rat snake (*Elaphe obsoletus*), bullsnake (*Pituophis melanoleucus*), speckled kingsnake, and ringneck snake (Conant & Collins 1998).

Predator Recognition

To determine if hispid pocket mice can recognize the scent of a predator snake and distinguish between scents of an allopatric predator species and a sympatric predator species, I conducted laboratory experiments in which pocket mice were exposed to different scent treatments.

Treatments were the scent of a sympatric predator snake, an allopatric predator snake, a non-predator snake, and a non-predator mammal. The sympatric predator snake for mice at SWMA and SLL was the diamondback rattlesnake. This species occurs at both localities with pocket mice and is abundant in Woodward Co. I encountered these snakes nightly while road cruising and found at least five on SWMA. The allopatric predator snake I used for laboratory interactions was the timber rattlesnake. The range of this species overlaps that of hispid pocket mice along the extreme western edge of its range and does not extend into Woodward Co. The capture locality closest to Woodward of timber rattlesnakes was recorded in the city of Covington in Garfield Co., Oklahoma, ca. 161 km NW of Woodward (Oklahoma Biological Survey, http://www.biosurvey.ou.edu/dokadesc.html).

For mice from STILL the sympatric and allopatric snake species were reversed: the timber rattlesnake was sympatric and the diamondback rattlesnake was allopatric. Timber rattlesnakes were common in Payne Co. and occurred in the same areas as hispid pocket mice, whereas the range of the diamondback rattlesnake did not extend into Payne Co. The capture locality closest to Stillwater of diamondback rattlesnakes was recorded in the city of Glenpool in Tulsa

Co., Oklahoma, ca. 97 km E of Stillwater (Oklahoma Biological Survey, http://www.biosurvey.ou.edu/dokadesc.html).

I used the ringneck snake as the non-predator snake for both groups of mice. This species is sympatric with pocket mice, abundant in Woodward Co. and Payne Co., and was used to test if mice could differentiate between odour of a control and non-predator snake. Scent of a non-predator mammal [white-tailed deer (*Odocoileus virginianus*) feces] was used to test if mice responded just to a novel odour.

Collecting Techniques

Timber and diamondback rattlesnakes were collected in Payne and Woodward Co., respectively. Ringneck snakes were collected in both counties. Deer feces were collected at SWMA. I housed rattlesnakes individually in 25-gal. containers and ringnecks together (two-five) in a 10-gal. aquarium. I preserved deer feces in a conventional freezer.

I collected pocket mice from each study site by setting 200-300 Sherman live traps in trap lines of 50 in grassland/shrub habitat. I set trap lines ≥ 10 m apart, placed traps 5 m apart within a trap line, and baited them

with rolled oats. I trapped at SWMA and STILL during summer and fall of 2002 and 2003 and at SLL during 2003.

I had 7,800 trap nights at SWMA and caught the hispid pocket mouse, deer mouse (n = 62), white-footed mouse (n = 61), hispid cotton rat (n = 60), fulvous harvest mouse (n = 34), silky pocket mouse (n = 22), eastern mole (n = 2), woodrat (n = 5), prairie vole (*Microtus ochrogaster*; n = 1), and northern grasshopper mouse (*Onychomys leucogaster*; n = 1). I had 800 trap nights at SLL and caught hispid pocket mouse, deer mouse (n = 19), white-footed mouse (n = 9), hispid cotton rat (n = 2), silky pocket mouse (n = 5), least shrew (*Cryptotis parva*; n = 1), woodrat (n = 4), northern grasshopper mouse (n = 18). I had 1,500 trap nights at STILL and caught the hispid pocket mouse, deer mouse (n = 36), white-footed mouse (n = 19), hispid cotton rat (n = 103), prairie vole (n = 1), and Eliot's short-tailed shrew (*Blarina hylophaga*; n = 1).

Chemosensory Trials

After capturing hispid pocket mice, I returned them to the laboratory and individually housed them in 10-gal. aquaria. I maintained them under a photoperiod similar to the light period that was naturally occurring at the time of collection. The exposure apparatus for laboratory trials is shown in Fig. 1. Tunnels were made of PVC pipe cut in

half with mesh wire on top. At the beginning of the entrance tunnel, there was an area with a door leading to the rest of the apparatus. At the end of the two Y-tunnels there was a 15-gal. plastic container. I presented each scent to mice by placing paper towels saturated with scent into the appropriate plastic container. I obtained substrate-borne odours of the three snake species by placing paper towels to be used in trials on the floors of cages in which snakes were held for ≥ 2 weeks. I did not use paper towels that held feces from snakes. I crushed deer feces and rubbed them into a paper towel. The control scent in each trial was a paper towel misted with deionized water. I misted all paper towels with deionized water so they would be as moist as control paper towels. I set up interactions so that a single mouse would be exposed to both a test scent and a control scent for a given trial. I cleaned the apparatus and containers after every trial and used paper towels with scents only once to ensure that the scent of the mouse and the treatment scent in a previous trial were not being detected. I used either tongs or gloves to handle all paper towels so that human odours did not confound the experiment.

I conducted trials ≥ 1 hour after sunset in low, red-light conditions. At the time of a trial, I transported a

mouse from its aquarium to the trial room in a mesh bag inside a paper bag so it was not exposed to bright light. I then placed the individual in the apparatus and allowed it to adjust for 3 minutes. After the 3-minute period, I removed the door leading to the rest of the apparatus by way of a string-pulley attachment from outside the trial room. I allowed the mouse to move through the apparatus for 5 minutes, then returned it to its aquarium.

I exposed mice to each of the four scents paired with the control. I did not use mice in the experiment more than once a day. I systematically assigned the order in which scents were presented so that each scent was in the same order position (ie. first, second, etc.) for the same number of times. I determined the side of the laboratory set-up in which the scented enclosure was placed by flipping a coin. I recorded animal responses on 8-mm video tape and then viewed tapes to quantify number of times each mouse completely entered control or scented chambers, proportion of time each mouse spent in control and scented areas of the laboratory set-up (defined as time spent in a given treatment divided by total time spent in the two chambers, excluding time spent in the arms of the lab set-up), and any other relevant behavioural patterns (e.g. defecating, grooming, freezing).

Analysis

Thirty-eight pocket mice were used in the trials: 15 mice were collected from SWMA, 17 from SLL, and six from STILL. Mice that did not perform (i.e., move out of the entrance tunnel) on more than two treatments were removed from analysis, which resulted in a sample of 20 mice from SWMA and SLL and four from STILL. Of the four mice from STILL, only two had complete trials (performed on all four treatments); therefore I did not perform statistical analyses on trials for mice from STILL.

I tested for order and position effects using two-way ANOVA's to determine if the order in which scents were presented to mice or the side of the apparatus in which scents were presented affected responses of mice. I then used repeated measures ANOVA's with each mouse as a repeated unit to analyze number of times each mouse entered control and scented chambers and proportion of total time each mouse spent in control and scented chambers. I used an arcsine square-root transformation on proportional data before analysis. Repeated measures ANOVA's were conducted by inserting each treatment scent and control individually so that there were 8 treatments. I then looked at Tukey's pairwise comparisons to determine significant differences between relevant treatment scents and corresponding

controls. I analyzed all data using SAS version 8.0 (SAS Institute Inc., 1999).

RESULTS

More time was spent with test scents than with controls except for ringneck snake scent (Fig. 2). Mice entered test scent and control chambers between four and five times per trial (Fig. 3).

All data sets were normally distributed and had equal variances. No differences were found for treatment/order interaction (F=0.54, df=9, P=0.8412), or order effects (F=1.52, df=3, P=0.2195), indicating that the order in which scents were presented did not affect mouse performance. No differences were found for treatment/side interaction (F=1.35, df=7, P=0.2317)or side (F=3.63, df=1, P=0.0592), signifying that mice did not prefer to spend more time on the right or left side of the trial apparatus just based on location. There was an overall significant difference in the number of times each scent was visited (P=0.0347); however, there were no significant differences between treatment scents and their corresponding controls (Table 1). An overall significant difference was found between time spent in each chamber (P=0.0046). Pocket mice spent significantly more time in chambers with timber

rattlesnake scent than control (P=0.0316) but no other significant differences in time spent in scent chambers were found (Table 2).

The most common behaviour recorded was defecation in the entrance tunnel during the adjustment period. Twenty mice defecated in the tunnel during 64 trials. Additionally, three mice left feces in the *C. atrox* chamber, one of those mice also defecated in the corresponding control chamber.

DISCUSSION

There were no significant differences in number of times pocket mice went into each scent chamber and its corresponding control. Mice generally ran back-and-forth between chambers and did not stay solely in one chamber for a given trial. There also were no differences between time spent in chambers with ringneck snakes or deer feces and their corresponding controls possibly because pocket mice do not recognize these scents as a threat.

The fact that there was no significant difference in time spent with sympatric diamondback rattlesnake scent and its control was unexpected. Most studies regarding rodent responses to snake scent have found one of two reactions: avoid scented areas or approach and investigate the scent

(see Kats & Dill 1998 and references therein). Results of this study suggest that pocket mice cannot recognize diamondback rattlesnake scent or they do not perceive this scent as a threat. Other means of avoiding snake predation such as selective microhabitat use may be employed (see Chapter 1). Several studies suggest that quadrupedal heteromyids restrict their activity to areas with vegetation to avoid avian predators (Rosenzweig 1973; Kotler 1984). However, those experiments were conducted in desert localities where vegetation was sparse. Because hispid pocket mice dwell in shrub and grassland environments, open areas may be safer from avian predators because vegetative cover is always nearby. Hispid pocket mice have been shown to prefer bare ground and short grass significantly more than tall grass and shrub microhabitat during times of the year when snakes are active (Ackland, 2004; Chapt. 1). This suggests that pocket mice use open areas to avoid coming into contact with snakes as has been shown for bipedal heteromyids. Bouskila (1995) found that *D. deserti* avoided bush habitat more than open habitat when the scent of a snake was present. Brown (1989) and Price (1978) showed that *D. merriami* preferred open habitat in summer but shifted preference to bush in winter.

Hispid pocket mice spent more time in chambers with allopatric timber rattlesnake scent than the corresponding control, which suggested that pocket mice sensed odours presented and possibly were investigating the unfamiliar scent. Rodents often investigate odours of predatory snakes (Hennessy & Owings 1978; Kobayashi 1987; Tamura 1989). Randall et al. (1995) demonstrated that the banner-tailed kangaroo rat (*Dipodomys spectablis*) investigated scents of the Mojave rattlesnake (*Crotalus scutulatus*) and gopher snake (*Pituophis melanoleucus*). However, both species are primary predators of kangaroo rats, so scents of these snakes should be familiar. It is possible that hispid pocket mice differentiate between sympatric snake scents and allopatric snake scents. Timber rattlesnake scent was unfamiliar to them and may have led them to inspect the scent and stay in chambers with that scent longer.

This study suggests that hispid pocket mice can distinguish between scent of a snake and a control (timber rattlesnake and corresponding control), but there is not sufficient evidence to determine if they can distinguish scents of predatory and non-predatory snakes. Pocket mice did react differently to scents of sympatric and allopatric rattlesnakes by spending significantly more time in

chambers with timber rattlesnake scent than the corresponding control. The fact that pocket mice showed no difference in time spent with diamondback rattlesnake scent compared with the control indicates that detection of chemosensory cues alone may not elicit avoidance or inspection of the scent. Pocket mice likely use other means of snake avoidance such as selective microhabitat use.

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Table 1-Results of Tukey's post-hoc test for number of times each scent chamber was visited.

Effect	df	t	P
C. atrox vs. control	85.9	-0.21	1
C. horridus vs. control	89.2	-0.85	0.9894
D. punctatus vs. control	89.3	0.85	0.9896
O. virginianus vs. control	91.3	-0.88	0.9872

Table 2-Results of Tukey's post-hoc test for time spent in each chamber.

Effect	df	t	P
C. atrox vs. control	65.1	1.43	0.8393
C. horridus vs. control	61.2	3.27	0.0316*
D. punctatus vs. control	62.3	-1.47	0.8226
O. virginianus vs. control	67.8	-0.39	0.9999

* Indicates significant difference ($P < 0.05$)

Figure Legend

Fig. 1. Laboratory apparatus used to test responses of hispid pocket mice to the odour of a sympatric predatory snake, allopatric predatory snake, non-predatory snake, and deer feces compared to a control scent of deionized water.

Fig. 2. Mean time spent in test scent and corresponding control chambers: timber rattlesnake, $n = 19$; diamondback rattlesnake, $n = 17$; ringneck snake, $n = 19$; deer feces, $n = 15$.

Fig. 3. Mean number of times mice entered test scent and corresponding control chambers: timber rattlesnake, $n = 19$; diamondback rattlesnake, $n = 17$; ringneck snake, $n = 19$; deer feces, $n = 15$.

Figure 1

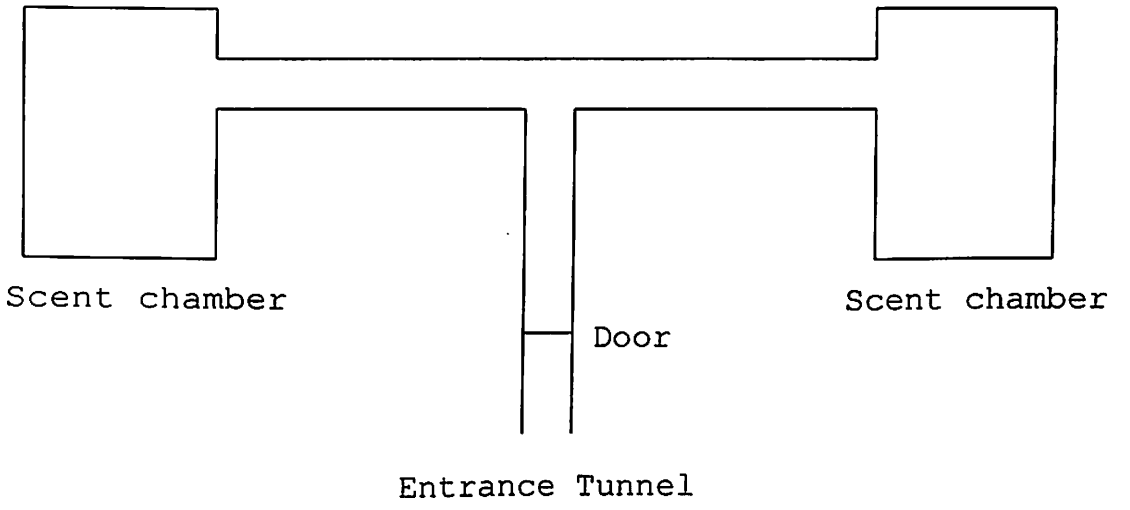


Figure 2

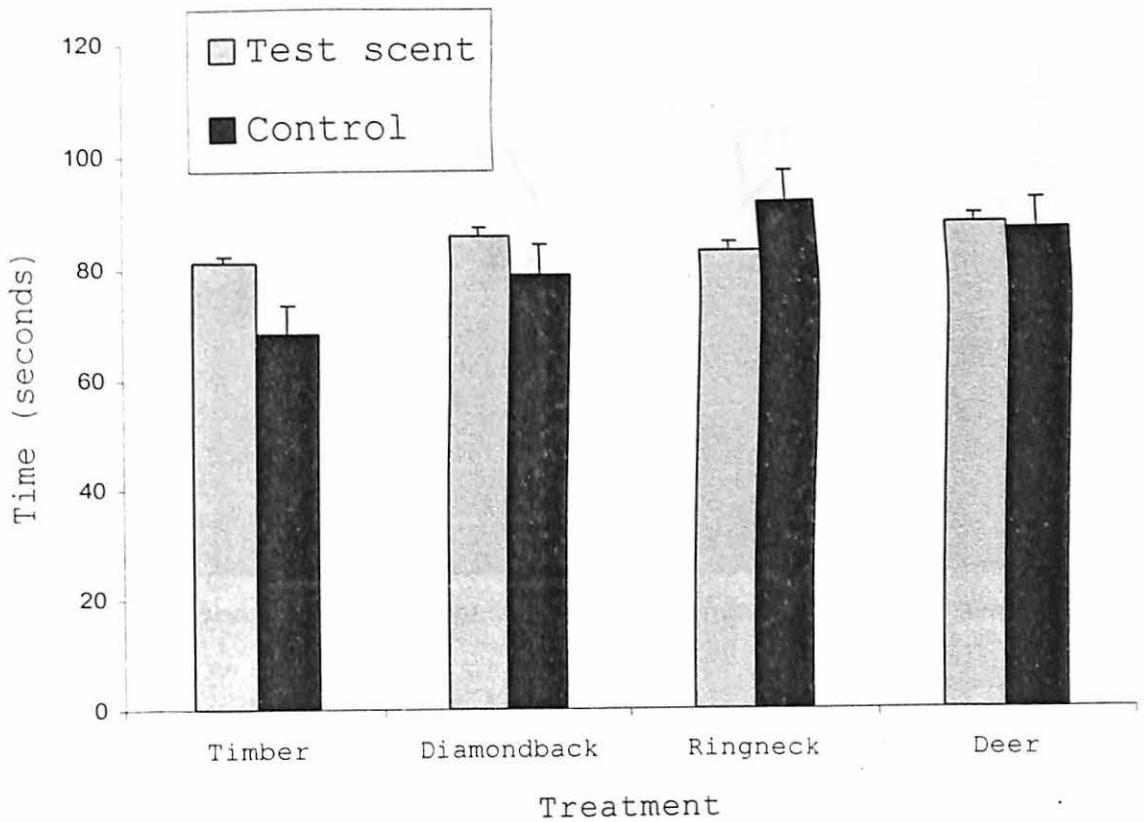
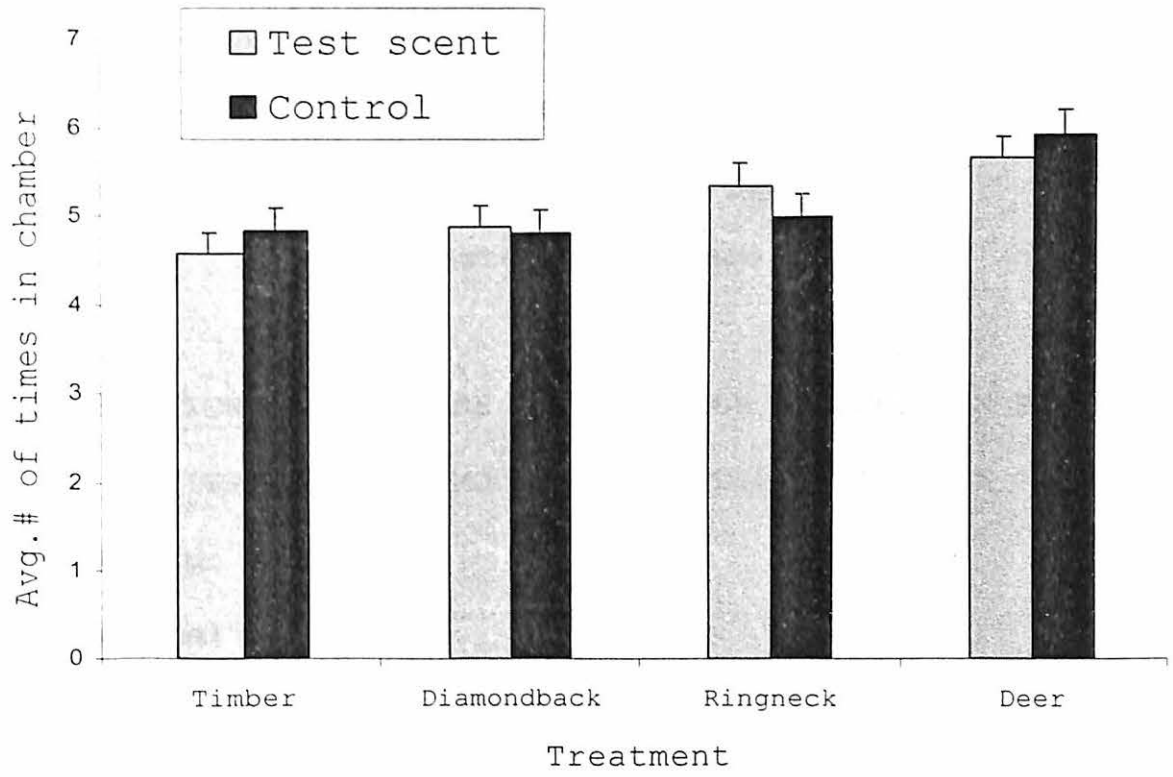

Test scent
Control
120
100
80
60
40
20
0
Time (seconds)
Timber
Diamondback
Ringneck
Deer
Treatment

Figure 3


Test scent
Control
Avg.# of times in chamber
0
1
2
3
4
5
6
7
Timber
Diamondback
Ringneck
Deer
Treatment

VITA

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